

Chapter 14



Ecological Perspectives on Pacific Salmon: Can We Sustain Biodiversity and Fisheries?

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Introduction

Pacific salmon *Oncorhynchus* spp. may arguably be the most studied group of exploited fishes. Yet, with many populations already extinct, a number listed as threatened or endangered, and many others depressed (Nehlsen et al. 1991; Slaney et al. 1996; NRC 1996a), biologists remain unable to answer critical questions for the public regarding sustainability of these salmon populations. Natural salmon production is significantly down in many of the remaining U.S. Pacific Northwest and some British Columbia populations, leading to significant reductions of important subsistence, commercial, and sport fisheries. Further, although many Alaskan and some British Columbia populations have been at all-time highs over the past several decades (e.g., Holmes and Burkett 1996; Wertheimer 1997), there have been serious declines during the past several years in some important Alaskan populations relative to record high previous years (e.g., Kruse 1998). The obvious question in light of these pervasive declines is: how can we sustain biodiversity and fisheries?

Sustaining Pacific salmon includes both recovery for listed populations and protecting and reinvigorating healthy populations (Huntington et al. 1996). A thorough understanding of the various aspects of salmon biodiversity is a basic requirement for sustainability. To find answers, we must explore the interplay between Pacific salmon ecology and human activities. We need to incorporate what we currently know into improved

management, both at the domestic and international levels. We also need to identify changes in research and management that are necessary to do a better job.

The purpose of this chapter is to describe how integrated awareness of key ecological concepts helps to explain the dramatic declines in salmon populations in some portions of their range, and why healthy runs are also susceptible to decline. The concepts also help create a framework that reveals the physical, ecological, political, social, and economic requirements for restoration and sustainability. These ideas are not necessarily new, but recent scientific and technological developments are rapidly providing an expanded basis for synthesized thinking about salmon management. Integration of these ideas into habitat and harvest management will be critical to the long-term survival of salmon populations and the fisheries they support.

Important Definitions for Ecological Perspectives of Pacific Salmon

To avoid ambiguity in the discussion of ecological concepts in this chapter, I define some core terms specific to this discussion of Pacific salmon:

Salmon ecosystem—The salmon ecosystem for each population includes every location where a given population occurs throughout its life cycle: the spawning location, freshwater rearing areas, all downstream migration waters, the estuary, nearshore marine habitats, oceanic regions where that population migrates, and all estuarine and freshwater upstream migration waters (Lichatowich et al. 1995; Hartman et al. 2000). This entire complex of habitats must be included when considering the health and management of each population. This implies that separate populations' ecosystems overlap in downriver, estuarine, and marine environments.

Sustainability—The long-term viability and productivity of aquatic ecosystems, natural population biodiversity, and biomass that support healthy aboriginal, sport, and commercial fisheries and vital communities throughout the range of salmon for generations to come (Kendall 1999; Knudsen et al. 2000a). Sustainability in this context is not to be confused with reliability or consistency. Significant fluctuations in abundance are part of the natural state of salmon populations (discussed further below).

Biodiversity—The naturally evolved (i.e., genetically based) array of hierarchical population structures (Allendorf and Waples 1995), life history strategies (Mangel 1994), phenotypes (Healey and Prince 1995), and

unique population production capacities (Pearcy 1992) exhibited by salmon. Most of the biodiversity in anadromous salmonids is based on local adaptation mediated largely by the habitats in their ecosystem as defined by their migratory and homing tendency.

Populations—The smallest freely interbreeding spawning aggregations not mixing with other populations, other than by natural background straying. These units are analogous to the demes described by Riddell (1993) and NRC (1996a).

Management unit—One or more populations, grouped together for management purposes such as setting escapement goals, managing for harvest rates, and implementing regulations (Knudsen 2000).

Key Ecological Concepts for Salmon Sustainability

Salmon populations, like all organisms, tend to expand their range and fully utilize available habitat through the evolution of survival strategies that allow them to be successful. This expansion is limited by the interplay of natural physical, hydrographic, and biological features, gradual climatic change, and short-term weather-induced events. Superimposing human-induced harvest, habitat alteration, and artificial salmon production on natural salmon systems reduces, constrains, or alters the populations' natural expansion capacities (NRC 1996a). I use four essential ecological concepts, relevant to natural expansion and constraint, to set the stage for understanding how human activities limit salmon production capacity and, more importantly, what steps can be taken to restore depleted populations and sustain healthy runs. The concepts are habitat suitability; population biodiversity; population biomass; and migrations, straying, and colonization.

Habitat Suitability

Salmon abundance and distribution are strongly influenced by basic habitat availability and by natural variation in the physical environment. Salmon populations gradually adapt to a variety of subtle habitat differences (e.g., Allendorf and Waples 1995). In the shorter term, favorable conditions allow expansion and population growth; unfavorable conditions constrain populations and production. Much has been written about the habitat requirements for successful salmon production (e.g., Groot and Margolis 1991). Several recent scientific developments, however, deserve emphasis here.

Riparian zones

Riparian zones provide salmon streams a connection to and a buffer from upland areas. These zones contribute to salmonid health by providing shade, streambank stabilization, sediment control, litter input, large woody debris, and nutrients (Spence et al. 1996 and references therein). The priority for riparian zones is to protect all existing healthy streamside areas (Dominguez and Cederholm 2000). For restoration, streamside vegetation should be replanted where necessary and protected from livestock grazing, agriculture, logging, urbanization, and heavy recreational use. Vegetation provides relatively short-term restoration and forms the basis for long-term riparian ecosystem function by anchoring streamside soils, providing overhanging and undercut streambanks, increasing habitat complexity, forming pools and braiding, enhancing flows between instream and hyporheic zones (Beschta 1997), and eventually supplying large woody debris to the stream system.

Riparian zones have been dramatically altered, often eliminated, in urban and suburban areas (Boule and Bierly 1987; Langer et al. 2000). Logging and agriculture have also substantially and extensively affected riparian areas (Gregory et al. 1987; NRC 1996a). Streambank destruction resulting from livestock grazing, channelization, logging in riparian areas, urbanization, and streamside recreation is extensive and profoundly reduces important physical stream habitat features, especially for juvenile salmonid rearing (NRC 1996a).

Instream habitat complexity

Despite inherent differences among streams and stream reaches, it is clear that habitat complexity and dynamics are important features of aquatic systems (see Spence et al. 1996 and Burger 2000 for reviews). Juvenile salmonids depend on a variety of depths, substrates, habitat structures, flows, and off-channel habitats to supply food, feeding stations, and cover. These features are usually present in streams having a variety of woody debris and pool/riffle configurations (e.g., Gregory and Bisson 1997). Adults depend on adequate depth, substrate, flows, and instream structure for upstream migration, cover while waiting to spawn, and successful spawning (e.g., Burger 2000). Complex stream structure also helps to retain organic material, essential to the nutritional basis of the aquatic ecosystem (Gregory et al. 1991).

Large wood is an essential construction vector that influences stream erosive forces, helping to create additional habitat complexity and spawning and rearing habitat (Cederholm et al. 1997; Beechie and Sibley 1997). Woody debris has been demonstrated as crucial for juvenile salmonids in

contributing to cover habitat, flood refuge, food production, and nutrient retention (e.g., Bryant 1983; Cederholm et al. 1997). Large wood has also been implicated in providing habitat diversity in estuarine and marine habitats (Sedell et al. 1988).

Natural habitat suitability has been greatly compromised through activities that reduce stream habitat complexity. Gregory and Bisson (1997) summarized studies that document broad-scale stream habitat simplification through reduction of large instream wood and complexity of pool habitats. Early logging depended on log driving, the practice of flushing logs downstream, as the preferred mode of transportation (Wendler and Deschamps 1955). Loggers removed as many obstacles from the streams as possible. Furthermore, large trees, the primary source of large instream wood, were logged and cleared from the streambanks and the rest of the watershed, resulting in a loss of future wood for natural stream restoration (Bisson et al. 1987). The logging industry later went through a shift to land transportation, during which much debris was allowed to accumulate in streams. Ironically, the recognition of this as a problem for fish passage and water quality (Bisson et al. 1987) eventually led to a period of stream cleaning when nearly all woody debris was again removed from some streams. The problem of too little or too much wood debris in streams has now been clarified, and most current forestry practices include consideration for maintaining large woody debris in streams. In many areas, however, the long-term needs for large wood remain unmet because of the lack of large trees in the riparian zone.

Habitat restoration has included instream wood replacement, with mixed success. Although many instream wood placement projects have either failed or have not shown increases in fish production (e.g., Frissell and Nawa 1992), a number of projects have demonstrated short-term benefits to both instream habitat complexity and density of stream-rearing salmonids (e.g., Peters et al. 1993; Cederholm et al. 1997). Additional research is needed to determine whether those local, short-term improvements translate into increased adult salmon production. As Dominguez and Cederholm (2000) point out, prior knowledge about salmonid requirements and fluvial geomorphic processes is required for successful habitat restoration. The limiting aspects of properly functioning stream and riparian ecosystems need to be considered to create habitats that provide the interim structural framework until riparian and upland forests recover from historical disturbances (Dominguez and Cederholm 2000).

Other activities that diminish habitat complexity—such as gravel mining, channelization, diking, riprap, and stream clearing for flood control—reduce the carrying capacity for salmonids (see Gregory and Bisson 1997 for review). Channelized small streams are generally less hospitable for larger

salmonids, although negative effects for all rearing salmonids increase with severity of channelization (Chapman and Knudsen 1980; Knudsen and Dilley 1987). Because of sampling difficulties, there has been no successful research on how channelization affects salmonid use in larger streams. However, studies demonstrating the importance of habitat complexity (e.g., Peters et al. 1993) imply that simplification of larger stream habitat during channelization likely reduces the carrying capacity for salmonids. Diking is especially harmful in lower stream reaches because it prevents access of juveniles to important off-channel rearing habitats (Beechie et al. 1994).

Channelization and diking aggravate flooding effects on fish survival because the flow volume and velocity are restricted to the channel areas rather than being dissipated into off-channel areas. The higher flows tend to scour substrate and wash woody debris out of the system. Diking and channelization also reduce flows between the river and the hyporheic zone (Stanford and Ward 1993).

Spawning substrate

Clean gravel with adequate interstitial water flows is essential for successful egg and fry incubation and survival (Groot and Margolis 1991 and citations therein). Natural spawning habitat is degraded by both gradual, nonpoint deliveries of fine sediments from agricultural, urban, and logging landscapes, as well as accelerated landslides and excessive streambank erosion caused by increased flooding from altered landscapes (NRC 1996a; Gregory and Bisson 1997). Selection of spawning locations is likely a heritable characteristic and, considering the subtleties of criteria for optimal spawning habitat, relatively minor changes in the nature of the streambed can make the habitat unsuitable. Road building, especially associated with logging activities, has accelerated the natural rate of streamside landslides that deliver excessive silt, sand, and gravel to streams (e.g., Harr and Nichols 1993). Spawning substrate can be too unstable or fine sediments can compact the interstices, making the substrate unusable (e.g., Hartman and Scrivener 1990; Montgomery et al. 1996). Incubating eggs and fry in the gravel are more easily dislodged if the substrate is too unstable.

The hyporheic zone

The hyporheic zone of rivers, the area where water flows under the sand and gravel substrate, is extremely critical (Edwards 1998). This zone is often the connection between groundwater and alluvial flows. The extent of this zone, together with the relative volume of river flow, can dictate the relationship between rainfall, snowmelt, and groundwater over the seasons. Hyporheic zones are biological hotspots that contain intensive physical and chemical gradients (Edwards 1998; Dahm et al. 1998). Although the true

extent is yet to be documented throughout the range of salmon, there are some important direct connections between upwelling and salmon success. For example, interior Alaskan chum salmon populations find incubation refuge from extreme winter weather in groundwater upwelling areas (Finn et al. 1998), and Hanford Reach chinook salmon *O. tshawytscha* spawn predominantly in areas of hyporheic discharge (Geist 2000). Furthermore, the movement of water, nutrients, and microorganisms into (downwelling) and out of (upwelling) the hyporheic zone is a critical ecological process in streams and lakes (Stanford 1998; Dahm et al. 1998) that likely has strong influence on the production processes upon which juvenile salmonids depend.

The biological importance of the hyporheic zone has been largely overlooked until recently. Physical changes—through gravel mining, channelization, diking, riprap, and flow alterations—have altered the groundwater/surface water interface (Stanford and Ward 1993). Reestablishing the natural channel configuration, which allows for natural amounts of woody debris for channel complexity, will be necessary for restoration of this important ecological interface (e.g., Wissmar and Beschta 1998).

Water quality and quantity

Salmon in every life history stage require water within acceptable temperature and oxygen levels and free of contaminants (Groot and Margolis 1991 and references therein). Thermal alterations potentially affect the survival and growth of every stage during the freshwater life cycle (NRC 1996a). Removal of riparian vegetation and changes in flow regimes have contributed to increased temperatures (May 1996). Many urban and suburban watersheds are being overloaded with nutrients, resulting in abnormal plankton blooms and oxygen deficiency (e.g., Fresh and Lucchetti 2000). Toxic chemicals, as well as nutrients, are washed into streams from urban and suburban landscapes, particularly under altered flood runoff patterns. Industrial activities continue to add toxic chemicals and oxygen-depleting nutrients to water bodies (e.g., Seiler 1989).

Runoff patterns critically influence the degree to which a given stream reach is conducive to salmon production. Timing and intensity of stream runoff greatly influence success or failure of instream production. Floods have been recognized as a beneficial and important vector in the long-term natural disturbance regime to which salmon have adapted (Bisson et al. 1997). Problems occur, however, when natural flow patterns are exaggerated by human-induced landscape changes. Watershed landscapes have been dramatically altered through logging, agriculture, and urban and suburban development. Removal of vegetation, increased impervious surfaces in urban and suburban areas, and flood control projects have led to major changes

in runoff patterns. In the short term, flooding can limit survival by disrupting spawning activity or dislodging incubating eggs or fry (see Gregory and Bisson 1997 for review). In the longer term, excessive flooding also alters stream morphology through erosion and increases the frequency of stream-side landslides, thereby increasing bedload movement and sedimentation to the detriment of salmon (Gregory and Bisson 1997 and references therein).

Urban areas particularly suffer from increased frequency and intensity of flooding (e.g., Fresh and Lucchetti 2000). Runoff patterns from agricultural and clear-cut landscapes have also changed. Increased likelihood of streambed scouring and resultant egg or alevin mortality are contributing to salmon population losses (Montgomery et al. 1996; Gregory and Bisson 1997). Increased flood flows also tend to wash important woody debris from rivers and streams and cause increased erosion of streambank habitats (Gregory and Bisson 1997).

Conversely, low flows can dewater redds, limit juvenile habitat, or preclude successful migrations (Hicks et al. 1991; NRC 1996a). Water that flows off altered landscapes more rapidly than unaltered watersheds not only causes increased frequency and intensity of flooding but is then unavailable to recharge groundwater, exacerbating summer low flows (Wissmar and Beschta 1998). Aquifers are the primary source for summer flows, an important determinant of the physical rearing habitat for juvenile salmon (Gregory and Bisson 1997).

Water is often removed from streams and rivers for municipal water supplies, agricultural irrigation, industry, and power generation, exacerbating the negative effects of natural low flows. Dewatered stream and river reaches have reduced spawning and rearing habitat as well as increased predation on juveniles, barriers to migration, and stream temperatures (NRC 1996a). For example, up to 50% mortality of juveniles was attributed to flows diverted from the Sacramento River (Kjelson and Brandes 1989). Furthermore, most of the removed water is not returned to the stream, and, of the water that is returned, most is substantially degraded (NRC 1996a). Varying discharges downstream of power production facilities result in stranding of juvenile salmon (Bradford 1997).

Systemic watershed health

Awareness of the importance of systemic watershed health is increasing. Functional watersheds provide a relatively stable mix of conditions conducive to salmon production and survival. For example, forested landscapes dampen the extremes of spawning substrate-scouring rain and snow runoff events (Wissmar and Beschta 1998), and forested riparian lands provide gradual input of habitat-creating large wood (Domiguez and Cederholm 2000). Disturbance at various scales is also part of the natural watershed

process (Bisson et al. 1997), but the cumulative effects of human changes to the landscape have in many cases dramatically exacerbated watershed disturbance to the detriment of salmon. Therefore, protection and restoration of watershed function depends on catchment-wide understanding of where problems occur and how to remediate them. Most now agree that specific instream restoration does not help unless the actions are integrated into a systemic watershed restoration program (e.g., Beschta 1997).

Systemic watershed health can be maintained by keeping intact the full range of aquatic and riparian conditions generated by natural disturbance events at landscape scales (Bisson et al. 1997), including actions that restore natural run-off patterns, recruitment of large wood to streams, and connections to off-channel habitats. Several authors have described important new approaches for watershed-oriented restoration (e.g., Bisson et al. 1997; Williams et al. 1999; Fresh and Lucchetti 2000). For example, Fresh and Lucchetti (2000) present a strategy for combining protection and restoration while considering the scale at which watershed functions occur. They emphasize the importance of considering how restorative or protective actions at one scale can either enhance or negate actions at another scale. Success depends largely on understanding the physical and biological dynamics among the scales as well as coordination among political jurisdictions. The new paradigm for watershed health appears to be an ecosystem approach (MacDonald et al. this volume) guided by watershed analysis together with adaptive learning (Naiman et al. 1992).

Arguably the single most effective habitat-oriented action for salmon sustainability is to protect existing good habitat (see Frissell 1993; Lichatowich et al. 2000). The refuge concept should attempt to create connectivity and coincide with areas of genetic resources (e.g., Thurow et al. 2000). Federal forests and wilderness areas already serve as a core of protected area (Sedell et al. 1997). The concept of preserving the few remaining key watersheds is crucial to maintenance and recovery (NRC 1996a; Bisson et al. 1997; Williams and Williams 1997). U.S. federal plans for recovery include identifying key watersheds for analysis and then restoring those watersheds located on federal lands that meet the following criteria: those having one or more anadromous fish populations at risk of extinction, those consisting of high quality remaining habitat, those that include degraded watersheds with a high potential for restoration, or any combination of the three (Williams and Williams 1997). Local governments must also implement protective measures for small watersheds threatened by encroaching urbanization. Counties and municipalities have tremendous influence over salmon habitat because their actions directly affect landuse patterns. Watershed function must be protected and improved where necessary through conservation easements and other protective measures that

maintain riparian and instream integrity (Fresh and Lucchetti 2000). Another shift is necessary, from simple prescribed-width buffers to identification and protection of critical and/or sensitive habitats, such as unstable slopes and off-channel habitats (NRC 1996a). These critical locations can be identified through processes such as watershed analysis (e.g., Armantrout 2000).

Changes in estuarine and marine habitat

Naturally complex estuarine habitats are important to juveniles on their way to the ocean (Simenstad et al. 1982). Estuaries are particularly important to chinook, chum *O. keta*, pink *O. gorbscha*, and coho *O. kisutch* salmon for rearing as they make the transition from freshwater to salt water (Simenstad et al. 1982). In many places, access to intertidal marshes has been eliminated, particularly through diking for agriculture and flood control and for urban port development (NRC 1996a). For example, Simenstad et al. (1982) determined that about 90% of estuarine habitat has been eliminated in many developed Puget Sound river deltas.

Extensive nonsalmonid fishing is physically altering marine benthic habitat, and marine food webs are being changed through removals of significant biomass in both directed and incidental fishing (e.g., NRC 1996b). Chemical pollution by persistent organics, heavy metals, and radioisotopes has been identified as cause for concern, at least in the Bering Sea (NRC 1996b). Though there are no definitive studies on the effects of these activities on salmonid production, concerns have been raised about reverberations through the marine ecosystem (e.g., NRC 1996b).

Marine productivity

The importance of marine productivity limitations for salmon is increasingly apparent. Marine survival and production of salmon have been correlated with oceanographic and marine productivity indices (Holtby et al. 1990; Beamish and Bouillon 1993; Percy 1997). There appears to be a marine carrying capacity that, in some cases, can be exceeded and that varies annually (variation discussed below). Density-dependent marine growth has been implied by Ishida et al. (1993) and Rogers and Ruggerone (1993), and there are indications that salmon survival is density-dependent (see Thomas and Mathisen 1993; Perry 1995; Hilborn and Eggers 2000). Further evidence for limits to marine carrying capacity includes recent progress indicating that seemingly small changes in the ocean environment can strongly affect marine survival (e.g., Welch et al. 1998). Also, studies of data from Japanese chum hatchery production indicate poor survival and reduced size of returning salmon at sea in years of large hatchery releases (e.g., Ishida et al. 1993). Hilborn and Eggers (2000) also listed early ma-

rine competition as one possible explanation for reduced wild pink salmon production in the face of large expansions in the Prince William Sound, Alaska, hatchery program.

Environmental variation

Interactions between habitat suitability and environmental fluctuations strongly influence survival at all life stages: spawning, incubation, rearing, marine foraging, and migration (e.g., Bisson et al. 1997). A critical concept here is scale. Salmon survival and production can be influenced locally by a single storm event, but also on much larger scales by gradual, long-term shifts in regional climate (e.g., Kruse 1998). Montgomery et al. (1996) concluded that chum salmon egg burial depths, just below the bedload scour depth at mean annual high flows, were probably a finely tuned adaptation. This implies that larger floods from a single event could wipe out a brood class by dislodging eggs from redds. In the long run, as climate fluctuates, the frequency and intensity of devastating floods will ebb and flow.

In the marine environment, salmon production appears to be related to fluctuations in climate on several important scales. There is evidence that upwelling, which exhibits tremendous annual variation, significantly influences survival of Oregon coastal coho (e.g., Pearcy 1997). The Pacific decadal oscillation has been identified as a cycle in which ocean conditions dramatically change approximately every 20 to 30 years, relative to salmon survival needs, and has strong influence on salmon production patterns (Hare et al. 1999). Recent work by Welch et al. (1998) has indicated that ocean growth and survival may be limited by warm temperatures and that long-term climate warming could push the southern boundary of temperature tolerance farther north, reducing the total range of suitable sockeye salmon *O. nerka* grazing habitat (Figure 1).

Uncertainty is an important characteristic of environmental fluctuations and their influence on salmon production (NRC 1996a; Francis 1997). We will continue to learn about the relationships between environment and salmon production, but we will never be able to predict with certainty what will happen over the next several salmon generations. Still, our predictive powers are improving; in 1997, the most recent El Niño event was predicted months in advance (O'Brien 1998). That is primarily because meteorologists had studied the links sufficiently to understand that when the equatorial low becomes established, the El Niño is likely to follow. I believe science and technology can gradually reduce ignorance and uncertainty about salmon production drivers. Until technical knowledge improves, though, we need to manage without full knowledge and consider the effects of uncertainty on our decisions (Francis 1997). Caution is also necessary when interpreting the causes of good or poor run returns, so that one

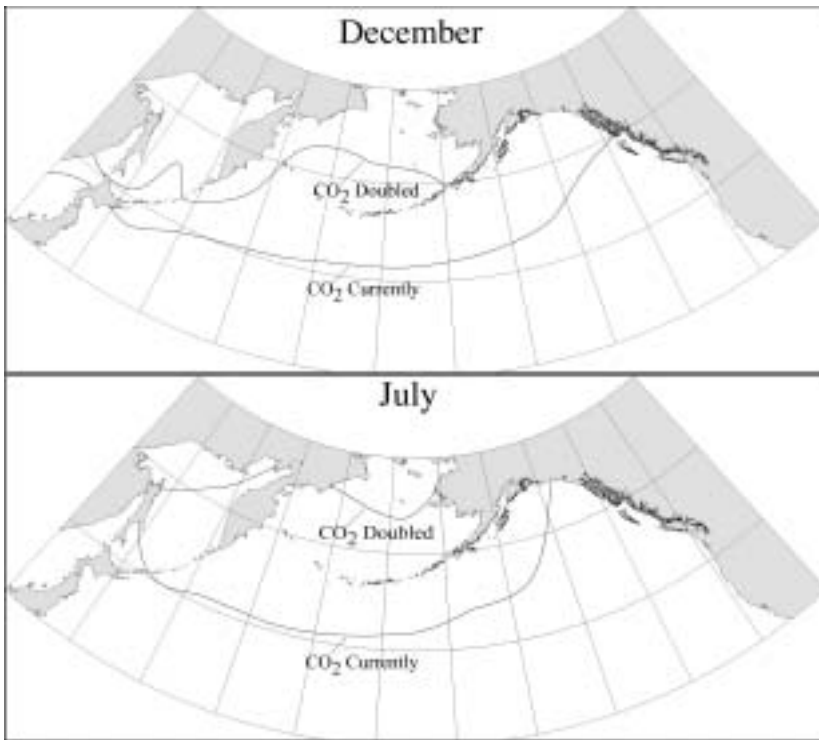


Figure 1. An illustration of how a doubling of atmospheric CO₂ might push the southern boundary of acceptable winter (top) and summer (bottom) sockeye salmon distribution northward, thereby seriously reducing the amount of marine habitat available for rearing (from Welch et al. 1998).

does not attribute them to the wrong factor. For example, one might falsely interpret habitat restoration as futile in years of poor marine survival (Hare et al. 1999).

Population Biodiversity

Local adaptation

Because of their tendency to home to their natal streams, Pacific salmon have evolved a diversity of genetic and phenotypic population characteristics (Waples 1991a). Every spawning population is potentially a unique genotype (Healey and Prince 1995); there is even evidence of genetically

based divergence within a single, relatively small spawning area (Woody et al. 2000). Examples of apparently heritable ecological strategies for success include variations in body size correlated with differences in stream flows (e.g., Beacham and Murray 1987), run timing for spawning and incubation survival (e.g., Smoker et al. 1998), duration of egg incubation (Woody 1998), and a variety of freshwater rearing strategies (e.g., Wood et al. 1987; Bisson et al. 1997).

That anadromous behavior is adapted to local and specific conditions is further evidenced by numerous failed attempts to establish self-sustaining runs of Pacific salmon through transplanting, at least within the native range (Withler 1982). Yet transplants of the nonanadromous form of sockeye salmon, kokanee, have often been successful (Wood 1995). Since numerous kokanee transplants have been successful while anadromous sockeye salmon transplants have generally not (Wood 1995), critical local adaptation apparently also includes the marine component of the salmon ecosystem. Successful transplants are apparently more likely if the habitat and geographic orientation of the watershed, relative to marine migrations, are similar to the habitat from which the donor population originated. For example, chinook salmon introduction into New Zealand rivers have been successful only in locations where the marine migration direction matches that of the donor population (T. Quinn, University of Washington, personal communication). The importance of local adaptation was further demonstrated in an unusually successful introduction of sockeye populations transplanted into previously unused habitat in Frazer Lake, Alaska. Genetic analysis determined that populations established themselves in spawning habitats most similar to their source habitat types (Burger et al. 2000).

Because salmon populations have gradually adapted to maximize survival in relation to subtleties in their habitat, changes in the habitat, such as those experienced in many Pacific Northwest locations, reduce the likelihood of long-term survival. Although populations could conceivably evolve to further adapt to the changes within several decades (Healey and Prince 1995), this will not occur at a pace in accordance with society's urgency to restore salmon sustainability. Because of the relationship between local adaptation and habitat, the appropriate conservation unit is the population within its habitat (Healey and Prince 1995). To maximize biodiversity and productivity, every population should be managed conservatively.

Hierarchical population structure

Numerous researchers (e.g., Reisenbichler et al. 1992; Riddell 1993; Wood 1995) have described the hierarchical nature of broad-scale genetic population structuring in salmon. Intraspecific genetic distance generally parallels geographical distance (Waples 1991a; Allendorf and Waples 1995). The

locally adapted populations are genetically more similar to their neighboring populations, resulting in a branched, hierarchical organization with populations grouped into metapopulations and metapopulations grouped into biological races (Riddell 1993). The races have been demonstrated at least on a relatively broad scale, to exhibit and be defined by significant intraspecific run timing differences within large watersheds (Allendorf and Waples 1995). Races tend to be more genetically different from one another than the differences among metapopulations within races, implying that the different run timings were based on unique historical colonization and evolutionary events (e.g., Utter et al. 1995; Burger et al. 1997).

The importance of individual, locally adapted populations to the long-term success of metapopulations should not be overlooked (Riddell 1993). As climate gradually changes or natural disturbances occur, they may be the basis for recolonization of habitat. Marginal populations may have a high adaptive significance to the metapopulation because they can contribute variation back into the central populations at times of contraction (Scudder 1989). The implications of local population differentiation and population structuring are important in fisheries management decisions regarding the scale at which populations are protected from habitat and harvest threats (Riddell 1993; NRC 1996a).

The diversity of Pacific salmon population structuring, as well as demographics, is clearly in peril in some areas. As of June 2000, there were 26 evolutionarily significant units (ESUs) listed under the U.S. Endangered Species Act (ESA) as threatened or endangered and another five candidate ESUs. Decisions about which populations to include in listings are based on the concept of the evolutionarily significant unit (ESU; Waples 1991b, 1995), which is often applied at the metapopulation, race, or multiple-race levels. There is, however, an important distinction between actions to prevent extinctions, as defined by ESA, and actions required for achieving sustainability. Whether the ESUs are listed or not, the ESA process will not solely prevent continued losses of local populations or demographic declines. Because ESUs are broadly defined, some constituent populations may effectively drop out, regardless of the overall performance of the ESU by ESA criteria. Sustainability requires activities that maintain and enhance diverse population substructuring through protecting all local populations, allowing continued local adaptation and maintaining adequate abundance.

Harvest impacts on biodiversity

Salmon management should be based on the premise that local reproductive populations are genetically different from one another and valuable to long-term salmon production (NRC 1996a). When harvesting reduces the number of adults reaching the spawning grounds, several aspects of

biodiversity can be affected. First, extinctions of local spawning populations (e.g., Walters and Cahoon 1985; Nehlsen et al. 1991) decrease the overall genetic and phenotypic diversity of populations, as well as the total biomass produced from conglomerate populations. Though the definition of reproductive isolation and the degree of protection afforded to recognizably different spawning populations remain debatable (Waples 1995), it is clear that some amount of diversity is lost with every lost population (Reisenbichler 1997). Genetic variation within and between the hierarchical levels of salmon population structure are the resource base for Pacific salmon, both for long-term sustainability and continuing evolutionary process, and it should be vigorously preserved (Riddell 1993).

Second, when harvest reduces a population to some minimum number of spawners, genetic diversity is threatened by inbreeding and/or genetic drift (Reisenbichler 1997). Resultant reduced fitness contributes to a downward spiral of survival, with the population simultaneously and increasingly more susceptible to random downturns in environmental variables causing poor survival (e.g., Lawson 1993). Minimum population sizes are impossible to estimate with certainty; the actual value likely varies among populations. Depending on the circumstances, however, even populations larger than 500 individuals may be at risk of extinction from these factors (Reisenbichler 1997). Genetic diversity is also threatened, even in abundant populations, by the selective forces of fishing—for example, by potentially changing run timing, spawn timing, size at age, or age of maturity (Reisenbichler 1997).

Third, the mixed-population fishery is a particularly challenging threat to population biodiversity. Many smaller, less productive populations can be chronically overharvested when harvest rates are set for entire management units based on spawner-recruit information for the more productive constituent populations (NRC 1996a; Knudsen 2000). Hatchery-reared populations are particularly troublesome because they can sustain very high harvest rates. The problem is worse the farther the fishery occurs from terminal spawning areas. As populations migrate toward natal streams, they separate from one another in time and space, potentially increasing the ability to harvest from various populations. Still, decisions are made to incidentally harvest commingled weak runs while targeting healthy runs, even in terminal area (Copes 2000). The ideal situation is either to harvest each population separately or to moderate harvest rates so as to not overharvest the least productive population in a mixture (e.g., Van Alen 2000). The latter is problematic because, in many cases, the weakest population can withstand only low or no harvest. This would result in foregoing harvest on other, possibly many, populations in the mixture. In practice, there are numerous combinations of management alternatives, ranging from a single

harvest rate for a large number of populations, as in Alaska (e.g., Van Alen 2000), to extensive closures to protect weak populations, as in Canadian coho conservation measures (Fisheries and Oceans Canada 1999). With notably declining run sizes and ESA listings, management scenarios are changing rapidly and extensively (e.g., WDFW 1999).

Hatchery impacts on biodiversity

Many authors have addressed the issues of how artificial enhancement can negatively affect natural populations (e.g., Krueger and May 1991; Hilborn 1992; NRC 1996a). Artificial enhancement can take a variety of forms along a continuum, from small-scale captive brood programs for maintaining and expanding the last vestiges of a dwindling population to augmentation projects designed to improve survival and production in a natural run to large production hatcheries. While most would agree on the need for rescuing dangerously depleted populations through artificial measures, debate has ensued over the social and biological costs and benefits of artificial production in projects designed primarily to produce more fish. Most of the following discussion pertains to artificial enhancement programs at the larger production end of the spectrum.

Artificial enhancement can result in genetic effects for both the population managed in the facility and neighboring populations (Campton 1995), although observed differences between wild and hatchery fish may be complicated by management decisions such as population transfers (Nielsen et al. 1994). Pacific salmon reared in hatcheries quickly become domesticated—they adapt to the unnatural conditions of the hatchery environment at the expense of adaptation for living in natural streams (Reisenbichler 1997). Genetic changes in hatchery populations result from: random drift, which can increase the proportion of individuals homozygous for deleterious recessive alleles, reducing fitness through inbreeding depression; selection, caused by both intentional selection of mating crosses, as well as natural selection for individuals better suited to hatchery survival; or the practice of crossing various, sometimes geographically distant, stocks within a single hatchery (Waples 1991a). Although these genetic changes may result in a population more amenable to hatchery rearing, hatchery fish often do not survive the marine environment as well as wild fish (NRC 1996a), and marine survival of hatchery fish may deteriorate with increasing generations in the hatchery (Reisenbichler 1997).

Deleterious genetic effects also occur when hatchery fish spawn with natural fish. This results not only when hatchery fish stray into natural populations, but especially when managers try to augment natural production with a hatchery population (Reisenbichler 1997). Waples (1991a) describes the deleterious effects of hybridization between two gene pools (hatch-

ery and wild) through reduction in genetic variation between populations, which tends to genetically homogenize populations away from their local adaptations, and outbreeding depression, which causes reduction in fitness, hence survival, when parental populations of increasing genetic distance are crossed.

Both inter- and intraspecific competition occur naturally for salmon in freshwater, estuarine, and marine environments (Fresh 1997). The release of hatchery fish complicates the natural limitations imposed by competition. Several important studies have demonstrated that juvenile hatchery fish displace wild fish in streams. Hatchery coho juveniles rearing in streams were found to outcompete wild fish for food (Nielsen 1994). A number of authors have attributed reductions in juvenile coho instream survival and densities to competition with hatchery fish (e.g., Nickelson et al. 1986; Flagg et al. 1995). Both Nickelson et al. (1986) and Flagg et al. (1995) speculated that observed decreases of wild juvenile coho in streams stocked with hatchery juveniles were likely due to the larger hatchery fish forcing wild fish from feeding locations. McMichael et al. (1997) found that residual hatchery steelhead *O. mykiss* had a negative effect on wild steelhead growth in semicontrolled conditions. Competition may be especially critical in estuarine and nearshore marine areas, where juveniles can encounter food limitations that limit growth and survival while they are spatially concentrated and have similar diets (Fresh 1997). If there are limits to Pacific Ocean carrying capacity for salmon, as discussed in the section on marine productivity, excessive hatchery releases may aggravate poor survival, at least in years when conditions limit production.

Wild strays of exotic Atlantic salmon *Salmo salar* into Pacific salmon habitats are of particular emerging concern. The number of escapees from aquacultural net pens, particularly in British Columbia, has been increasing recently. Natural spawning and rearing have recently been confirmed, raising concerns about negative competitive impacts on native Pacific salmon (Volpe et al. 2000).

The effects of genetic dilution and competition are often exacerbated when natural populations in the area around the hatchery are struggling to survive in the face of high hatchery harvest rates. The case of Lower Columbia River coho salmon serves as a good example. That region has been managed for hatchery production, despite extensive quality coho habitat in the area. When it was recognized that very few truly wild coho remained in the streams and a petition for ESA listing was considered, genetic analysis could not detect wild from hatchery fish. The fish found in local streams likely were mostly hatchery strays (Wright 1993). For these and other reasons, primarily related to various hatchery practices throughout the region, Lower Columbia coho salmon were not listed under ESA (Flagg et al. 1995),

but only because any remaining wild fish could not be discerned from hatchery fish. Furthermore, the extensive habitat remains mostly devoid of natural production.

Population Biomass

The ecological importance of Pacific salmon spawning biomass to the freshwater environment may have often been overlooked (e.g., Cederholm et al. 1999; Gresh et al. 2000). Spawner-recruit models, upon which salmon management has depended for decades, tell us that limits to natural reproductive capacity can be not only be affected by too few spawners, but also that too many spawners can actually reduce production through density-dependent mortality (Ricker 1975). Returning adults that exceed the perceived capacity of the spawning and/or rearing habitat have traditionally been considered surplus available for harvest. With very little data or research on natural, unexploited salmon populations, however, it is possible that the so-called surplus may actually serve purposes previously misunderstood.

Carcasses as nutrients

Recent scientific evidence has shown that salmon carcasses provide a significant source of nutrients to freshwater ecosystems (Cederholm et al. 1989; Kline et al. 1993; Bilby et al. 1996; Cederholm et al. 1999). Not only do the carcasses support the basis of a nutrient pathway via primary production, but flesh and eggs are directly consumed by aquatic insects (Wipfli et al. 1999) and by rearing fish (Bilby et al. 1996). This biological feedback loop thereby ensures future salmon production.

Carcasses also supply nutrients to streamside vegetation (Ben-David et al. 1998) and wildlife such as bears, martens, eagles, and even songbirds (Willson and Halupka 1995; Ben-David et al. 1997; Hildebrand et al. in press). Retention of carcasses within the freshwater system is also critical to maintaining their effectiveness as a basis for production (Cederholm et al. 1989). When large woody debris is reduced in stream habitats, the network of carcass-trapping physical structure is eliminated.

Probably the most important implication for Pacific salmon is that the production relationship (returning adults per spawner) is influenced not only by the number of eggs deposited in the gravel, but also by the amount of biomass delivered and retained in the watershed (e.g., Cederholm et al. 1999). The carrying capacity for freshwater production depends on both the physical space available and the amount of nutrients provided to the system. This varies, depending on the freshwater life history of the species and the nutrient interdependence among species, but, in any case, there is a feedback mechanism relating the number of adults allowed to escape har-

vest directly to the productivity of the system. This biological control factor must be considered in the spawner-recruit relationship.

Freshwater carrying capacity

One seemingly inexorable problem in Pacific salmon management is the difficulty of truly understanding the capability of the freshwater habitat to support salmon production. Current observations are limited to populations that are subject to exploitation, have had their habitats altered, or some of both. Inferential estimates have been made of much greater historic salmon production in areas now altered by some amount of habitat degradation (Chapman 1986; Michael 1998; Gresh et al. 2000). But even where habitat is pristine, without observations of unexploited spawners and smolts, there is no sure way of knowing production potential. Theory behind spawner-recruit models tells us that the model expresses the population's expansion capacity, the spawners required for one-to-one replacement, and the spawning escapement at which production is maximized *if the model includes a wide array of escapement and production values and the data are accurate* (Hilborn and Walters 1992). Unfortunately, data for the vast majority of populations do not include values prior to exploitation that define the true equilibrium replacement point on the curve.

Recent technological advancements support reevaluating the efficacy of the spawner-recruit relationship for salmon. For example, core samples of marine-derived nitrogen in Karluk Lake, Alaska, sediments, presumably from sockeye salmon carcasses, were well-correlated with sockeye salmon harvest records during the recent 100 years and therefore could be extended as a salmon production surrogate back 300 years (Finney et al. 2000). These data indicate that salmon run sizes declined significantly and stayed lower during the most recent 100 years of exploitation (Schmidt et al. 1998; Finney et al. 2000). The nutrient data also supported recommendations for increased escapement goals relative to those estimated from spawner-recruit modeling with exploited population data alone (Schmidt et al. 1998).

I used the basic concept of these important findings to test a hypothesis: that the spawner-recruit model equilibrium point may be underestimated when the model is based on data collected after exploitation has begun. I generated hypothetical but realistic data for a salmon population before and after exploitation (Figure 2A). Spawner-recruit relationships were then plotted for the unexploited population (Figure 2B) to compare with the spawner-recruit relationship after exploitation (Figure 2C). One can easily see that the production of recruits under exploitation is much lower than when the population is pristine, *from exactly the same habitat*.

This is thought to result from the fact that fewer nutrients are entering the system to support freshwater growth and survival, thereby essentially

reducing the carrying capacity, even in a physically unaltered watershed (Cederholm et al. 1999 and references therein). From a management perspective, the situation has been exacerbated because a Ricker model of the exploited population, without knowledge of the true equilibrium point (i.e., carrying capacity), may provide erroneously low estimates of escapement at maximum sustainable yield (MSY) but that appear to make sense. When the reduced escapement goal is implemented, it aggravates the nutrient deficiencies, thereby further reducing production and setting the stage for sequential reductions in the escapement goals. I believe this management error is pervasive throughout the geographic range of Pacific salmon, depending variously on species and local management scenarios. This dynamic is preventing attainment of full sustainability and helps explain why populations are declining, even in locations with healthy habitat. When the biological downward spiral is combined with habitat alteration, the effect is even more dramatic.

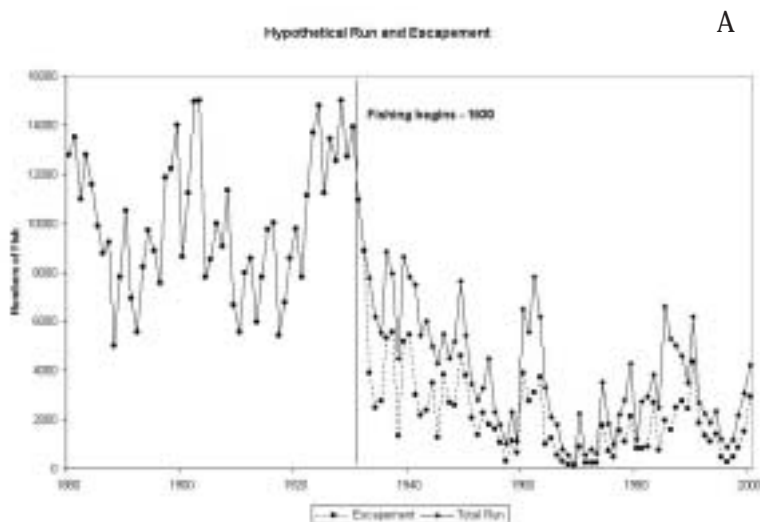
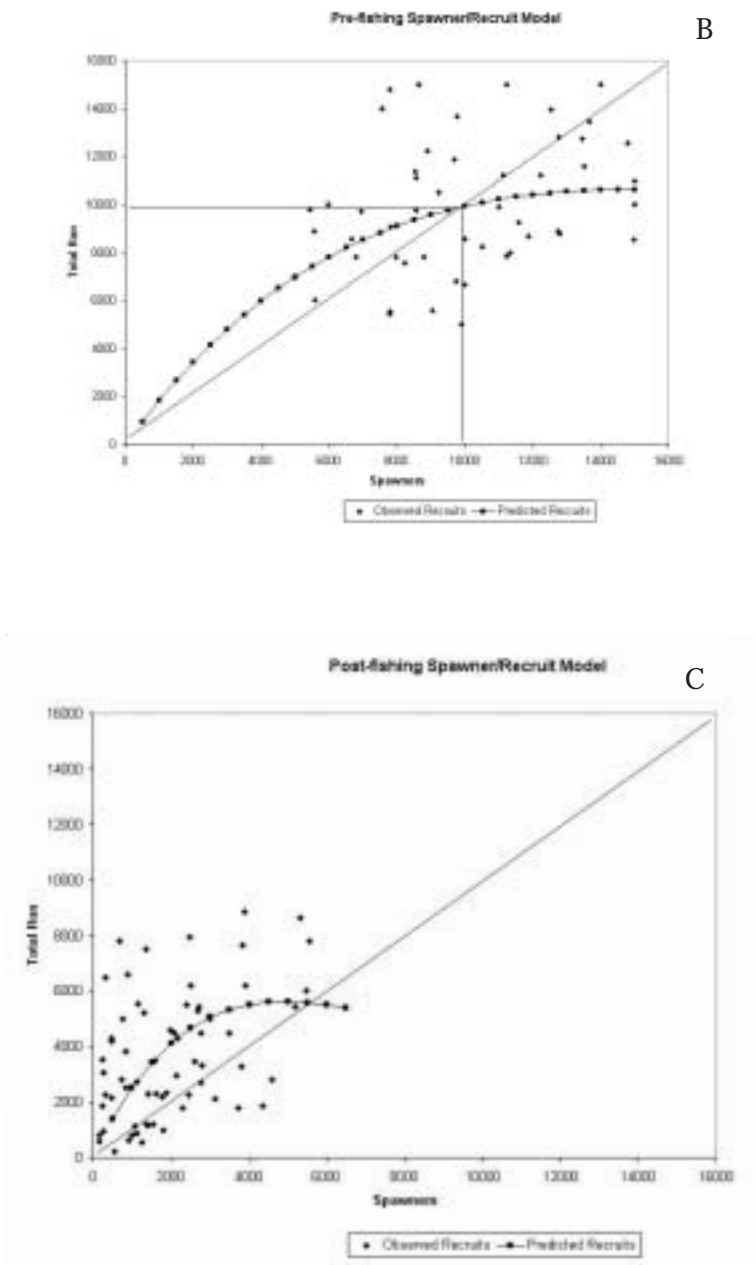


Figure 2. A: Hypothetical escapement and total run size data of a salmon population before and after fishing ensues. B: Spawner-recruit relationship before fishing begins. The data are spread around the equilibrium population replacement point, which defines the freshwater system's capacity to produce salmon when it is fully seeded and fertilized. C: Spawner-recruit relationship for the period of fishing. Notice the estimated MSY spawners are much fewer than before fishing (B), and the calculated equilibrium point is dramatically less even though the physical habitat is still the same.



Natural production buffer

The number of recruits produced per spawner can vary by more than an order of magnitude (Cramer 2000). Spawner-recruit models tend to average that variation and incorporate it into a simplistic view of the relationship. The most common outcome of the simple spawner-recruit relationship is a tendency to overestimate the exploitation rate and underestimate the spawning escapement needed for perpetuation (Hilborn and Walters 1992; NRC 1996a). Some of the perceived "excess" in run sizes may in actuality be a hedge against those years when natural, constraining disturbances occur (Hare et al. 1999). Although spawner-recruit models indicate that too many spawners may somewhat diminish production of the next cohort, there are often years when floods, drought, or poor marine food production will reduce survival, making extra spawners critical to long-term production. Straightforward use of spawner-recruit models for predicting harvestable surplus also does not account for measurement error (Hilborn and Walters 1992; NRC 1996a; Cramer 2000).

Harvest management implications

We have become accustomed to assuming that every salmon population has a quantifiable and reliable surplus production that can be harvested each year, that the only factors determining production capacity are the number of parents and the physical space required for spawning and rearing, and that humans are the only harvesters of returning adult salmon. Sustainable salmon populations will require a new escapement management paradigm that includes allowances for seeding of the freshwater incubation and rearing habitat, annual run size variability, carcass biomass to support optimal freshwater carrying capacity, and food for wildlife (e.g., Michael 1998).

Salmon harvest management is complex and difficult, fraught with challenges caused by inaccurate or insufficient data (Knudsen 2000), poor predictive models (Knudsen 2000), and a complex state, tribal, federal, and international management structure (Rutter 1997; MacDonald et al. this volume). Today's salmon management challenges range from the dilemma of too many salmon, such as in some southeastern Alaska fisheries, to populations in dire straits with only a few remaining individuals. In all cases, managers share the common problems of poor data, weak models, poor understanding of production capacity, uncertainty about factors controlling future production, and difficulties in managing fishing effort to optimize harvest while ensuring adequate escapement. Furthermore, decisions to harvest salmon can sometimes be too strongly influenced by the desire to fish as opposed to the need to conserve (Fraidenburg and Lincoln 1985).

Ocean variability has strong influences on salmon escapement (NRC 1996a). It is critically important that harvest rates be adjusted accordingly, so that adequate escapements can be met even in years of low ocean survival (Lawson 1993). This may mean low or no harvest in years of poor ocean survival, but this is a key to sustainability (NRC 1996a). Maintaining optimal freshwater habitat seeding in all years will ensure the best smolt production, hence the greatest possible marine production, given variable marine survival.

Migrations, Straying, and Colonization

A final natural ecological attribute of Pacific salmon is their tendency to migrate to and throughout the ocean, return home to natal spawning areas, variably stray and mix with other populations, and colonize new habitats. These extensive migrations are a hallmark of salmon, thought to enhance reproduction and survival by allowing a fish to take advantage of the greater marine food supply, resulting in larger body size, which is useful for extensive upstream migrations and in digging deeper redds, also benefiting survival of eggs and fry.

Upstream migrations

Pacific salmon may spawn anywhere from the intertidal zone of stream mouths, as in a few pink and chum populations, to the upper reaches of huge watersheds sometimes more than 1,500 km from the ocean. Successful reproduction obviously depends on unimpeded upstream access. Blocks to migration prevent adults from reaching spawning grounds, preclude offspring from using rearing areas, and cause mortality of juveniles moving downstream. The most notable losses are caused by main-stem dams on large rivers (e.g., Hassemer et al. 1997), although dams erected for power generation, water control, irrigation, or shipping enhancement on any size stream have resulted in significant losses (NRC 1996a). Some large dams have completely blocked access to extensive upstream areas. At other large dams, upstream passage facilities are less than fully effective and/or migrants suffer from "fallback" (NRC 1996a). Small dams and other barriers have been blamed for the extirpation of some runs (NRC 1996a). Culverts and other types of road construction have also often created migration barriers.

A unique and relatively unstudied source of upstream migration mortality may be attributable to various forms of catch-and-release angling. Limited studies on sport catch and release of chinook salmon indicate 10% or less direct hooking mortality (Bendock and Alexandersdottir 1993). However, because salmon have evolved marine feeding behaviors to acquire

a finite energy resource for their nonfeeding upstream migration and spawning, it is conceivable that females subjected to one or more capture-and-release events may prematurely expire before depositing their full complement of eggs into the gravel. This topic should be further researched. Although not specifically attributable to upstream mortality, additional research is also required for the effects of capture and subsequent release of salmon in nonretention commercial fisheries. Wertheimer (1988) estimated 25% mortality of chinook caught and released in troll fisheries. Candy et al. (1996) also estimated about 23% short-term mortality of chinook caught and released from purse seiners targeting other species. They also noted that viable released salmon remained in the area for the subsequent 24 h and consequently were susceptible to multiple captures. Future population models should account for these fisheries-induced mortalities.

Downstream migrations

Smolts moving downstream suffer extensive natural losses due to predation, competition for food, stranding by variable flow levels, and inaccessibility to offstream rearing habitats. These natural mortalities are exaggerated by human activities of dams, diversions, and diking. Mortality of downstream migrants passing through turbines, from gas supersaturation, or from increased predation, can be extreme at large, main-stem dams, and the effects are compounded if they must pass through multiple dams (e.g., Raymond 1988). Juvenile salmonids are subjected to stranding due to flow reductions downstream of water diversions and hydroelectric installations (e.g., Bradford et al. 1995). Downstream migrating juveniles are also lost into all sizes of unscreened or poorly screened diversions (e.g., Kjelson and Brandes 1989). Numerous studies have established the importance of off-channel freshwater and estuarine rearing habitats (e.g., Swales and Levings 1989). Culverts and road construction have been shown to block upstream access of juveniles to important off-channel rearing habitat (NRC 1996a). Dikes and levees built to create agricultural land from former wetlands or control floods also block access to juvenile rearing areas (e.g., Beechie et al. 1994).

Natural straying and colonization

There are abundant data indicating that, although salmon possess a strong natural tendency to home to the natal stream, most salmon populations exhibit some degree of natural straying to nonnatal spawning locations (see Quinn 1993 for review). Stray rates tend to vary substantially among and within species and among locations (Quinn 1993). The ecological significance of straying is thought to help perpetuate genetic diversity, but it may also be important for establishing new populations or revitalizing populations faltering after a sudden or long-term ecological setback. Populations

geographically closer to each other may tend to intermingle somewhat more than those farther apart (e.g., Klamath River chinook, as described by NRC 1996a). Natural straying for colonization of vacant habitats enhances larger escapements to neighboring streams (NRC 1996a).

Anadromous salmonids appear to be well adapted to reinvading areas of suitable habitat (Bisson et al. 1997). Adults are strong swimmers with high fecundity, and juveniles often disperse widely in search of productive rearing habitats (Groot and Margolis 1991). Research in Glacier Bay, Alaska, has revealed the rapid anadromous salmonid colonization of habitats recently exposed by retreating glaciers (Milner and Bailey 1989). Pink salmon and coho salmon juveniles have been found rearing in streams as young as 40 years (author's data). These findings imply that salmon will colonize suitable habitat as soon as their straying nature allows a spawning population to become established. Streams naturally exhibit ecological succession (Milner et al. 2000). If streams are at all amenable to salmonid colonization (i.e., having appropriate gradient and substrate and no insurmountable barriers), they gradually become increasingly suitable for colonization. Emigrants from established populations can then occupy this seemingly marginal habitat in which productivity would normally be low but which feasibly can become better than in source locations (Scudder 1989). As anadromous salmonids become established, their carcasses supply nutrients important to the further biological development of the system (Milner et al. 2000). Streams that have been altered by humans have the same potential to recover through natural processes, become more available for colonization, and have salmon gradually reestablish themselves.

When harvest rates are high, the absolute numbers of possible strays to nonnatal streams are reduced. Successful restoration may ultimately depend on colonization by strays. Relative abundance of returning runs is important to successful colonization because, assuming the stray rate is constant, the absolute numbers of strays to neighboring streams depend on the run size (Riddell 1993). Seemingly good habitat in some locations remains unused, probably because insufficient strays have been available to colonize habitat. If escapements to nearby streams were sufficient to supply the strays, we would expect to see fish straying into and colonizing unused habitats.

Achieving Sustainability

Pacific salmon sustainability, both of the biological populations and the socially and economically important fisheries that depend on them, requires a significant paradigm shift that emphasizes naturally functioning watershed ecosystems, with allowance for natural variation and diversity (Frissell et al. 1997; MacDonald et al. 2000). Recovery and/or perpetuation of healthy salmon systems also depends on whether fisheries managers, decision mak-

ers, and the public are willing to support certain protective and remedial actions. Several key, recent publications have provided both the background and specifics required for sustainability (see NRC 1996a; Stouder et al. 1997; Williams et al. 1999; Knudsen et al. 2000b).

Numerous fishery, habitat, and artificial production practices can and should be implemented to restore and maintain sustainable populations. Because the deleterious forces are multifaceted, the recovery and maintenance process requires action on all fronts simultaneously. Table 1 indicates, in broad categories, the kinds of management activities that should be considered for every salmon population. This table includes only general recommendations on each topic; expanded details will be required for population-specific remedies or protection measures. References cited are known examples that contain more specific information on each strategic management topic. Managers should carefully evaluate the requirements for recovery or maintenance of each population. It is essential that all relevant actions for each population be invoked simultaneously—leaving even one limiting factor unaddressed will prevent success.

Can We Sustain Salmon Biodiversity and Fisheries?

In summary, just as salmon populations exhibit incredible diversity in the extent of their range, life history strategies, and productive capacities, there is also much diversity in the types and extent of ecological insults that salmon populations face. Almost no populations remain unexploited. Most are subjected to some degree of harvest, habitat, or hatchery threat. Without widespread restorative action, some populations will thrive, but many will falter or even disappear. It will be a constant battle to keep struggling populations from declining further or disappearing and to ensure that healthier populations achieve full production and maintain sustainability.

So, how would we answer the question “can we sustain salmon biodiversity and fisheries?” I believe it is possible to do so. An affirmative outcome will depend, however, on society choosing a combination of actions that allow salmon to become and remain a thriving component of the ecosystem. With the four ecological concepts and related topics described above as a framework, society can make choices that minimize negative effects on salmon and, more often than not, actually benefit salmon. I believe the review presented in this paper and in recent volumes on the subject (especially NRC 1996a; Stouder et al. 1997; Knudsen et al. 2000b) demonstrate that scientists and managers have sufficient understanding of what salmon need, what diminishes them, and what could be done to protect and restore them. This does not reduce the need for increased scientific research to improve our abilities—numerous technological and informa-

Table 1. Generalized management activities that, when implemented simultaneously as appropriate for each population, should lead to recovery and sustainability of healthy salmon populations and fisheries.

Ecosystem and life history requirements	Management activity		
	Habitat management	Harvest and population management	Artificial production and stocking
Habitat suitability	Protect watersheds through salmon refuges and other methods ^{1,2} .	Ensure sufficient escapement to fully seed all available rearing habitat ³ .	Use the most local populations for supplementation ^{9,10} .
Systemic watershed health	Prevent further destruction of freshwater, estuarine, and marine habitats ³ . Use watershed analysis Use watershed analysis to prescribe protection and restoration needs ⁴ . Restore degraded watershed functions ^{4,5,6} . Ameliorate extremes in runoff patterns ⁶ . Protect and restore critical habitats, such as off-channel rearing areas ^{7,8} .		Supplement, when necessary, with populations with phenotypically similar life history ¹¹ .
Riparian zones	Maintain substantial streamside buffers ⁴ . Repair habitats where appropriate ¹² .		
Instream habitat complexity	Restore and/or maintain healthy watersheds and buffer zones ⁴ . Add wood where appropriate ^{12, 13} .	Include salmon carcasses in considerations of stream complexity ¹⁴ .	
Spawning substrate	Prevent gravel removal. Manage watersheds to reduce human-induced intensity and frequency of flooding and associated erosion ¹⁵ .	Ensure sufficient spawners to use all available substrate. Ensure sufficient spawners to maintain spawning substrate quality ¹⁶ .	
Hyporheic zone	Maintain natural flows and groundwater recharge patterns ⁴ . Repair and prevent	Ensure sufficient carcasses to fertilize the hyporheic zone ¹⁷ .	

Table 1. continued.

Ecosystem and life history requirements	Management activity		
	Habitat management	Harvest and population management	Artificial production and stocking
	alterations of stream-banks and riparian zones to maintain uninterrupted hyporheic zones ⁴ .		
Water quality and quantity	<p>Manage watershed for natural hydrologic regime to prevent extreme floods and maintain summer flows⁶.</p> <p>Ensure adequate flows for instream spawning, incubation, and rearing¹⁸.</p> <p>Ensure sufficient water is supplied to off-channel rearing habitats¹⁹.</p>	<p>Allow sufficient spawners to replace nutrients required for aquatic productivity²⁰.</p>	<p>Ensure that fish cultural operations do not reduce water quality.</p>
Estuarine and marine habitats	<p>Prevent any further losses of estuarine and intertidal habitats²¹.</p> <p>Maintain and restore access to habitats²².</p>		
Marine productivity		<p>Ensure maximum natural smolt production²³.</p>	<p>Minimize hatchery smolt releases where necessary²⁴.</p>
Environmental variation	<p>Repair and protect all local spawning and rearing habitats.</p>	<p>Maximize smolts, especially in periods poor marine survival²⁵.</p> <p>Increase research to account for variability in predictive production models, setting escapement goals, fishery economics²⁶.</p>	
Production bottlenecks	<p>Identify whether production bottlenecks are habitat-limited²³.</p> <p>Take corrective action where possible.</p>	<p>Be sure production is not limited by too few spawners for maximizing recruits or supplying nutrients to the system²⁷.</p>	<p>Ensure that natural production is not limited by competition from hatchery populations^{28,29}.</p>

Table1. continued.

Ecosystem and life history requirements	Management activity		
	Habitat management	Harvest and population management	Artificial production and stocking
			Prevent overfishing of natural populations in mixed fisheries with hatchery populations ¹⁹ .
Population biodiversity Local adaptation	Protect local spawning and rearing habitats ³⁰ .	Ensure sufficient spawners to all possible spawning habitats ¹⁹ .	Use only the most local populations for supplementation ³³ .
		Consider genetic refuges as possible recolonization sources ^{31, 10} .	Use hatchery supplementation of wild populations only as a temporary fix ⁹ .
		Align harvest management units more closely with specific populations ³² .	If supplementation is used, consider harvest implications for other local populations in the same fishery ²⁸ .
Hierarchical population structure	Protect all local spawning and rearing habitats ³⁰ .	Shift harvest emphasis toward maximizing all populations of spawners in their habitats ³⁴ .	Do not supplement one local population without consideration for genetic and abundance-based impacts on other local populations ¹⁹ .
		Reduce the number of populations in each management unit ²⁶ .	Minimize differences between hatchery and wild fish ³⁵ .
		Account for differences in population productivities in harvest management ²⁶ .	Minimize interbreeding by hatchery and wild fish ³⁵ .
			Use conservation hatcheries to propagate populations in jeopardy ³⁶ .
			Ensure that all hatchery operations have carefully defined objectives, including monitoring and evaluation ²⁸ .

Table 1. continued.

Ecosystem and life history requirements	Management activity		
	Habitat management	Harvest and population management	Artificial production and stocking
Biomass and productivity Maximizing escapements and production.	Protect and repair all local spawning and rearing habitats to ensure production opportunities ^{23, 25} .	Harvest a fixed proportion, rather than a fixed number, and never fish below the minimum biological escapement threshold ¹⁹ . Improve escapement goal methods ²⁶ . Improve catch and escapement data quality ²⁶ . Increase target specificity of fisheries including selective fisheries ¹⁹ . Continue and expand quotas and limited entry ²⁶ . Improve accuracy of in-season management ²⁶ .	Locate hatcheries only in areas where harvest of hatchery fish will not affect wild populations ^{19, 28} .
Carcasses as nutrients	Consider fertilizer supplied by carcasses as a part of the freshwater habitat ³⁷ .	Maximize spawners to all possible spawning habitats. Implement research to determine target levels required for full nutrient levels ³⁷ . Temporarily fertilize where necessary to restore production ²⁰ .	Distribute excess carcasses to local streams where appropriate.
Freshwater carrying capacity	Maintain quality of and access to freshwater habitat ^{23, 25} . Conduct additional research on carrying capacity, including considerations for freshwater nutrients ²⁶ .	Ensure sufficient spawners to seed all available spawning and rearing habitat ²⁷ . Conduct additional research on predictive models to optimize escapements and, ultimately, harvests ²⁶ .	Minimize competition between hatchery and wild fish ³⁸ .

Table 1. continued.

Ecosystem and life history requirements	Management activity		
	Habitat management	Harvest and population management	Artificial production and stocking
Natural production buffer	Protect all local spawning and rearing habitats ^{23, 25} .	Account for poor production conditions in escapement goals ³⁹ . Ensure sufficient escapement to meet wildlife needs ³⁷ .	Minimize hatchery smolt releases where necessary to avoid competition in years of low productivity ⁴⁰ .
Migrations, straying, and colonization	Ensure access to all possible spawning areas ¹⁹ . Improve passage at existing facilities ¹⁹ .	Allow sufficient escapement to colonize newly opened areas.	Preferably use only locally adapted populations for restoration ^{43, 11} .
Upstream migration	Remove dams where necessary ^{41, 42} .		
Downstream migration	Reduce mortalities at mainstem dams ^{19, 5} . Ensure access to all possible rearing areas and create habitat where appropriate ^{7, 22} . Reduce losses in diversions ¹⁹ . Open access to off-channel freshwater and estuarine rearing areas ²² .		
Straying	Protect all local spawning and rearing habitats ^{23, 25} .	Maximize spawners to increase the absolute numbers of strays ¹⁹ .	Prevent straying of non-native populations into native populations ³⁵ .
Colonization	Repair and protect all local spawning and rearing habitats ^{23, 25} .	Maximize spawners to increase the absolute number of strays into new, restored, and vacant habitats ¹⁹ .	Consider the trade-offs between natural recolonization and introduction of non-native populations ^{9, 11} . If non-native introductions are made, use geographically closest populations having phenotypically similar life histories ¹¹ .

1. Frissell 1993. 2. Lichatowich et al. 2000. 3. Williams and Williams 1997. 4. Bisson et al. 1997. 5. Williams et al. 1999. 6. Fresh and Luchetti 2000. 7. Cederholm et al. 1988. 8. Richards et al. 1992. 9. Allendorf and Waples 1995. 10. Thurow et al. 2000. 11. Burger et al. 2000. 12. Beschta 1997.

Table 1. continued.

13. Dominguez and Cederholm 2000. 14. Cederholm et al. 2000. 15. Gregory and Bisson 1997. 16. Montgomery et al. 1996. 17. Ben-David et al. 1998. 18. Beecher 1995. 19. NRC 1996a. 20. Stockner et al. 2000. 21. Levings 2000. 22. Beechie et al. 1994. 23. Lawson 1993. 24. Hilborn and Eggers 2000. 25. Hare et al. 1999. 26. Knudsen 2000. 27. Michael 1998. 28. Hilborn 1999. 29. Hilborn and Eggers 2000. 30. Healey and Prince 1995. 31. Li et al. 1995. 32. Mundy et al. 1995. 33. Hard et al. 1995. 34. Hyatt and Riddell 2000. 35. Resisenbichler 1997. 36. Stickney 1994. 37. Cederholm et al. 1999. 38. McMichael et al. 2000. 39. Cramer 2000. 40. Francis 1997. 41. Wunderlich et al. 1994. 42. Marmorek and Peters 1997. 43. Riddell 1993.

tion deficiencies have been described in this chapter. It does mean, however, that we can and should do everything possible to support salmon recovery and sustainability now, based on the best current information, while further research and monitoring build and enhance the information base.

Ideally, each population would be managed independently with a firm understanding of its production capacity, the spawning escapement required for perpetuation, and the harvestable surplus. The population would also be managed in the context of the watershed and ecosystem in which it evolved (Healey and Prince 1995; Fresh and Lucchetti 2000). The new paradigm appears to be a salmon life history ecosystem approach guided by watershed analysis together with adaptive learning (Naiman et al. 1992; Williams et al. 1999; Williams and Williams 1997; McDonald et al., this volume).

The challenges, then, lie in the realm of the public process. Probably the single most important issue is the matter of priority. Recent ESA listings in the Pacific Northwestern, and the public response to those listings seem to indicate that most people place a relatively high priority on maintenance and recovery of salmon. Another positive development is the recent accord under the Pacific Salmon Treaty that led to reductions of fisheries to help rebuild runs in both Canada and the United States. Further progress will depend on positive outcomes of difficult decisions on such diverse and seemingly disconnected topics as local land use, growth management, alternative power generation, and societal changes in fishing communities, among many others. Success will be achieved when humans can bring their economic and social systems back into harmony with the natural system that supports salmon. That transition depends on a combination of community involvement and public will to provide the necessary support for effective management programs and new science (MacDonald et al. this volume). If these things fall into place, salmon populations will thrive wherever their biological needs are met and their tolerance limits are not exceeded. The biodiversity of salmon populations and the continuation of healthy fisheries can be sustained if we value our ecological heritage

sufficiently to protect and repair watersheds, ensure healthy escapements, and preserve the genetic integrity of salmon populations.

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